Stridulation in *Palpimanus gibbulus* Dufour (Araneae: Palpimanidae)

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Stridulation in *Palpimanus gibbulus* Dufour (Araneae: Palpimanidae). - Individuals of *Palpimanus gibbulus* Dufour, 1820 from the Mediterranean islands of Naxos (Greece) and Sardinia (Italy) were found to stridulate when disturbed. The stridulatory organ belongs to the file-and-scraper type with the pars stridens on the outer face of the chelicera and the plectrum on the femur of the pedipalpus. The sounds are audible to the human ear from a very short distance only. They were recorded using an inductive transducer. The stridulatory signals were of a simple temporal structure, rather irregular and showed no marked frequency gaps. Power maxima were at 1.00 kHz and 2.42 kHz. Upper end of frequency range was at 8 kHz.

In *P. gibbulus* both sexes engage in sound production. Stridulation in *P. gibbulus* apparently serves at least a two-fold purpose: firstly, as a potential defence mechanism and secondly, in intraspecific communication. However, during courtship and mating, only males were clearly observed to stridulate.

Key-words: sound production - stridulation - communication - Palpimanidae - bioacoustics - morphology - courtship - behaviour.

INTRODUCTION

Sound production in spiders has been reported for 26 families (UETZ & STRATTON 1982) and various descriptions of morphological structures probably related to sound production indicate it may be even more widespread. The methods of

sound production are 1) stridulation (friction of rigid body parts), 2) percussion (striking the substratum) and, more rarely 3) vibration (oscillation of leg or body). Here, we focus exclusively on stridulation and refer those interested in other methods of sound production to UETZ & STRATTON (1982).

Although stridulation has been reported in 22 spider families (Uetz & Stratton 1982), only few studies have investigated the behavioural context in which it occurs, with the exception of the Theridiidae and Lycosidae (e.g. BRAUN 1956; GWINNER-HANKE 1970; STRATTON & UETZ 1983). Stridulation requires the movement of one body part (the plectrum or scraper) across a second body part (pars stridens or file). The location of file and scraper on the body of the spiders varies widely: there are 12 different types of mechanisms classified according to the location of the sound-producing structures (STARCK 1985, based on LEGENDRE 1963). It is assumed therefore that stridulation has evolved independently several times in spiders.

In the detailed surveys of LEGENDRE (1963) and STARCK (1985) the Palpimanidae are not listed as stridulating spiders, which is possibly due to the limited distribution and rare occurrence of the Palpimanidae. To our knowledge there is only little information on stridulation in this taxon: LAWRENCE (1962) named a *Palpimanus* species from the Namib desert *Palpimanus stridulans* and described its stridulatory organ morphologically. BRIGNOLI (1980) mentioned a stridulatory file on the chelicerae of an undetermined Palpimanus female from Sardinia but provided no further information on shape or structural details.

MATERIALS AND METHODS

The specimens examined belong to *Palpimanus gibbulus* Dufour, 1820. Although DUFOUR described the species as "*P. gibullus*", this is best regarded as a lapsus according to PLATNICK (1981). DUFOUR described the prosoma in Latin as hunch-backed ("thorace gibbo") which confirms the validity of the species name, *P. gibbulus*, used in the vast majority of citations.

P. gibbulus individuals were found in pine forests under stones or pieces of bark lying on the ground. The spiders were clinging to stones when these were picked up. Adults and juveniles of *P. gibbulus* were collected from Rhodos (Greece) in 1987, from the Cyclade island of Naxos (Greece) in 1990 and from Sardinia (Italy) in 1992, 1993 and 1994. Individuals from Sardinia were reared and kept in the laboratory in small plastic boxes containing a layer of gypsum and a piece of bark from their original locality. They were fed with nymphs and juveniles of the cellar spider *Pholcus phalangioides* (Fuesslin, 1775).

For morphological investigation 6 specimens preserved in ethanol from Naxos, Rhodos and Sardinia were dehydrated in a graded series of ethanol, critical-point dried, sputter-coated with gold and examined with a Zeiss Semco Nanolab 7 and a Hitachi S2460N SEM.

In order to investigate the behavioural context of stridulaton, the reaction of female and male *P. gibbulus* to disturbances (pinching, pushing) was observed.

Additionally, mating behaviour of 3 females and 2 males from Sardinia was studied. Males were brought to female boxes and behaviour was registered during the course of the following 2 hours. All individuals used for mating experiments were taken to the laboratory as adults. None of the juvenile individuals collected from the field reached maturity in the laboratory.

For bioacoustic investigations a light-weight magnet glued onto the spider's prosoma in combination with a magneto-dynamic vibration transducer was used (constructed by Th. Rollenhagen, Berlin: see STRÜBING & ROLLENHAGEN 1988). Spiders were disturbed with tweezers to evoke defence stridulation which was recorded by a stereo tape recorder (Sony WM D6C). Sounds were visualized with a spectrum analyser (Spectro 2000, MEDAV) which produced an on-line Fast Fourier Transformation visible on a colour monitor. For further analysis, records were sampled into a computer (Tandon 486/33, Compaq) via an analog-digital converter (DT2821, Data Translation) and analysed with signal processing software (Hypersignal Acoustic, Hyperception Inc.).

RESULTS

Morphology

The stridulatory apparatus of *P. gibbulus* belongs to the chelicera-pedipalp type with the file situated laterally on the chelicera and the plectrum on the inner side of the pedipalp (fig. 1A). Both sexes possess a stridulatory apparatus. The morphology of the file appeared uniform in all individuals investigated, i.e. neither a sexual dimorphism nor differences between populations were apparent (figs. 1C, 1D). The stridulatory file extends 580 - 620 µm along the surface of the chelicera and consists of two areas, a proximal area (180 - 200 µm) the surface of which is undulated (figs. 1C, 1D) and consists of small parallel ribs (ca. 0.5 µm thick and 2 µm high) and a distal smooth area of larger parallel ribs (fig. 1B) which covers about 400 µm. These ribs are about 1µm wide at the top and around 3.5 µm at the base and 3 - 5 µm high.

The plectrum is situated on the pedipalp, i.e. on the inner lateral surface of the femur and is composed of several modified setal bases (fig. 2A). Figure 2C shows the arrangement of the plectrum: a row of bristles starts proximally on the femur and continues halfway along its longitudinal axis. The bases of the bristles are enlarged and sharp-edged (fig. 2B). The bases are 7 - 13 µm high and 7 - 10 µm broad. The plectra of the specimens from Rhodos appeared to be slightly smoother in shape, but the difference between populations was not marked. The morphology of the plectra is not sexually dimorphic.

Behaviour

When handling a live *P. gibbulus* female, one of us (GU) was alerted to the up and down movements of the spider's pedipalps. Movements of both palps were not in phase. Holding the spider close to the ear, a faint, high-pitched buzz was audible.
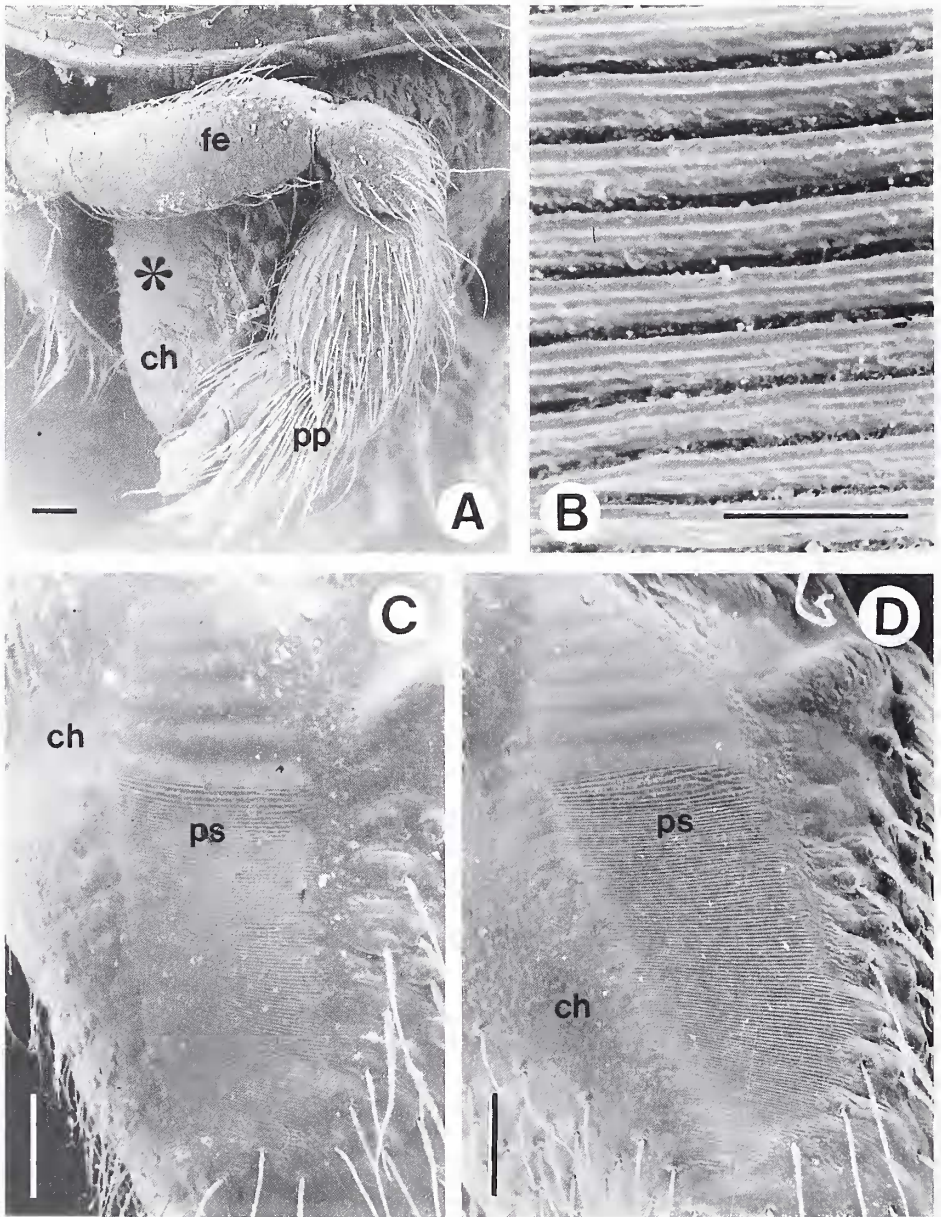
FIG. 1

A: Stridulatory apparatus of *P. gibbulus* (male from Sardinia), * position of stridulatory file. Scale line = 100 µm. B: stridulatory file, detail of the large ribs (female from Sardinia) Scale line = 10 µm. C: stridulatory file (male from Sardinia). Scale line = 100 µm. D: stridulatory file (female from Naxos). Scale line = 100 µm. ch: chelicerae; fe: femur; pp: pedipalpus; ps: pars stridens.
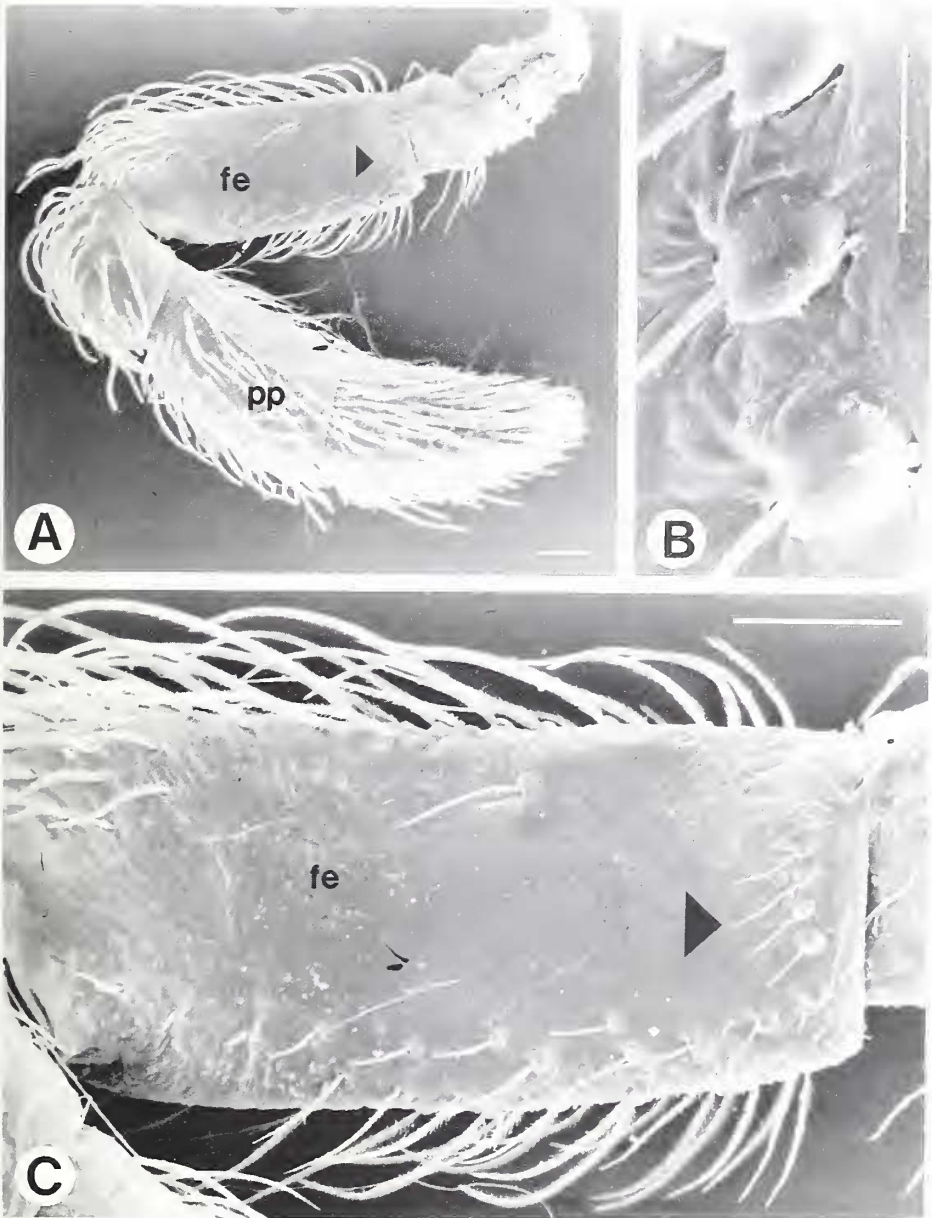
FIG. 2

A: Pedipalpus of *P. gibbulus* female from Sardinia, inner side. Arrow pointing towards plectrum. Scale line = 100 µm. B: Bristle bases on the plectrum. Scale line = 10 µm. C: Detail of the pedipalpal femur with row of bristles indicated by arrow. Scale line = 100 µm. fe: femur; pp: pedipalp.

Individual transferred to the laboratory stridulated as a reaction towards pinching, pushing or handling in general. Defence stridulation is usually accompanied by a threat position, whereby the large first pair of legs is raised. They possess a unique arrangement of spatulate hairs prolaterally on the tibia, metatarsus and tarsus (see figs. 279, 281 in FORSTER & PLATNICK 1984). In the following description of mating behaviour we refer to "stridulation" whenever the typical palpal movements occurred, although the sound is not audible from the distance necessary for undisturbed observation.

Mating was observed with 2 females and 1 male in 1992 and 1 female and 1 male in 1994. The females from 1992 did not allow copulation, although the male courted them. Courtship apparently commenced only after the first contact between the partners which appeared to occur by chance while the individuals moved about inside the box. After initial contact, females in both pairs stridulated. The male approached each of the females, touched them, retreated and stridulated from a distance of about 1 cm. The pair from 1994 engaged in a single copulation: after the male encountered the female face to face, he moved on to her prosoma, stridulated and quivered with his abdomen. The female moved slightly, lifted her first pair of legs and quivered with the second pair of legs. Whether the female stridulated as well could not be observed, as the mounted male concealed the view. The male moved onto the opisthosoma of the female who then quivered with increasing amplitude with her first and second pair of legs, stridulated briefly and lifted her body upwards into a
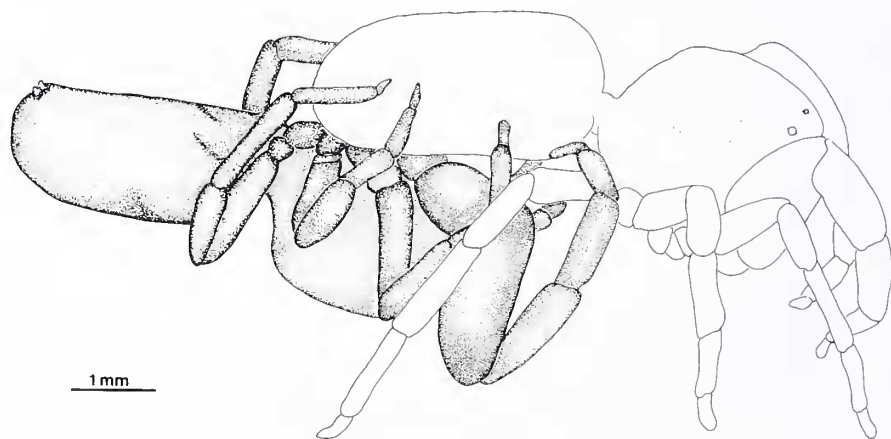

FIG. 3

Copulatory posture of *P. gibbulus*, drawn from a photograph taken by C. Gack. Female above, male below. Female pedipalps concealed by the large, first pair of legs. Male pedipalps are partially shown adjacent to the femur-patella joint of the female's fourth leg.

'tiptoe' position. Then the male turned to a parallel position and moved underneath the female who stayed in the tiptoe position. After a pause of about 40 s the male tapped the female with his second and third pair of legs while his large, first pair of legs served as a holdfast: the male's "knee" (femur-patella joint) was pressed against the ground whereas leg 4 of the female was clamped between his tibia and tarsus of leg 1 which are both well equipped with scopulae. The male's fourth pair of legs pressed against the caudal part of the female's opisthosoma. Copulation took place in this position (fig. 3). Before insertion, the male was observed to stridulate. Insertion of the palps took place in succession with the palps wriggling slightly during the first minute of insertion. After thirty-five minutes the female started to move, causing the male to jerk back and forth and then sideways with his entire body but without removing the inserted palp. The male again tapped the female with his second and third pair of legs and jerked. The female resumed movement, the male apparently withdrew the inserted palp and stridulated briefly. The female became increasingly active and carried the male still clinging to her around. 57 minutes after insertion the male loosened his hold, but remained close to the female in an antiparallel position and tapped her with his first pair of legs before separating.

Bioacoustics

Only stridulatory signals produced under artificial stimulation could be recorded. These signals show a simple and irregular temporal structure (figs. 4A, B) and a relatively homogeneous power spectrum (fig. 4C). Normally, the spiders produced a complex chirp caused by an upstroke and a downstroke of the pedipalp. We were not able to detect in which direction pedipalp movement started. The two strokes can be recognized in the chirps at ca. 10 ms, 45 ms and 70 ms. At ca. 55 ms a single up or downstroke was made and the corresponding down or upstroke was partly suppressed. Its traces can be seen at 60-65 ms.

The sonagram (fig. 4B) shows that the main frequency band (between 0.9 kHz and 1.4 kHz) of the signals was slightly tuned downwards from about 1.4 kHz to 1.1 kHz in the course of each chirp.

The power spectrum (fig. 4C) shows no frequency gap, only a shallow depression at ca. 1.8 kHz. Consequently, two power maxima can be identified: the first at 1.00 kHz, the second at 2.42 kHz. The upper end of the frequency range is ca. 8 kHz.

DISCUSSION

The chelicera-pedipalp stridulatory apparatus of *Palpimanus gibbulus* is classified as type d according to LEGENDRE (1963). Following this classification, the apparatus of *P. gibbulus* belongs to type dII, named "organe de Simon" after SIMON, who first described this organ type in the genus *Sicarius* in 1893. According to a later classification by STARCK (1985), the apparatus of *P. gibbulus* would be classified as a type d1 organ. The morphology of the stridulatory apparatus of *P. gibbulus* is very
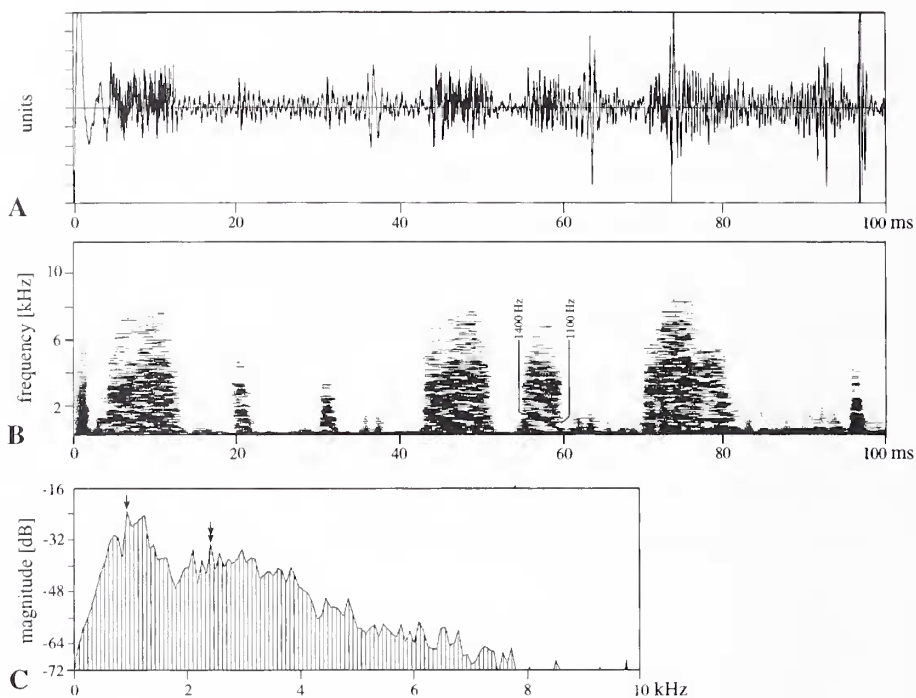
FIG. 4

A: Oscillogram, B: sonagram and C: power spectrum of stridulatory sound of a *P. gibbulus* female from Sardinia. In A and B the chirps at ca. 10, 45 and 75 ms represent sounds produced by an up and downstroke of the pedipalp, while the chirp at ca. 55 ms was caused by an isolated up or downstroke. In B, the slightly tuned main frequency band is marked for the chirp at ca. 55 ms. The vertical axis in C is scaled in relative units. No attempt was made to calibrate the sound energy measurement. The arrow points to the first power maximum at 1.00 kHz, the double arrow to the second at 2.42 kHz.

similar to the apparatus described for *P. stridulans* by LAWRENCE in 1963. A yet unpublished SEM studies by N. Platnick (pers. comm. 1995) demonstrate that at least three American palpimanid species (*Anisaedus stridulans* González, *Anisaedus pellucidae* Platnick, *Otiothops lauus* Platnick) also have cheliceral stridulatory ridges. The chelicera-pedipalp stridulatory apparatus seems to be the prevalant mode of sound production in Palpimanidae.

In *P. gibbulus*, stridulation is employed in at least two different behavioural contexts: defence and intersexual communication. Juveniles and adults of both sexes engage in sound production when attacked or otherwise disturbed, whereas only males unequivocally stridulate during courtship and copulation. With regard to females, the situation is not as clear: both females that did not mate exhibited stridulation on the first encounter with a male. This could have been a defence reaction as

well as intersexual communication. In the pair that engaged in mating, the female stridulated briefly during courtship however significantly less than the male. Since only one complete mating could be observed, it remains unclear whether the observed difference represents the typical mating behaviour of *P. gibbulus*. Whether stridulation is used in the context of male-male aggression as in the Theridiid spider *Steatoda bipunctata* (GWINNER-HANKE 1970) also remains an open question, because no more than one male was available at a time. Unfortunately, Palpimanids occur at low population densities, thus making a more detailed investigation difficult.

Bioacoustics

The simple and irregular temporal structure of the stridulatory signals as well as the lack of any marked frequency gap indicate that these chirps are disturbance signals (cf. MASTERS 1980). Typical intraspecific stridulatory signals are highly regular, possess a complex temporal pattern (BAILEY 1991:104, grasshopper songs) and show marked frequency gaps (RIEDE & KROKER 1995, cicada songs). However, we cannot exclude the possibility that *P. gibbulus* produces different sounds in the context of intraspecific communication, e.g. by a different movement pattern of the pedipalp or by scraping over another part of the file, e.g. the proximal portion only (fig. 1).

The sonagrams look similar to those from sounds produced by a double stroke of a file-and-scraper organ, e.g. in the longicorn beetle *Dorcadion fuliginator* (SCHMITT & TRAUE 1990). The slightly downward tuning of the main frequency band is probably without a biological meaning since each single stroke in a backwards-and-forwards movement has to slow down at the turning point, which inevitably leads to a frequency modulation that is observed regularly in stridulatory sounds, e.g. in criocerine leaf beetles (SCHMITT & TRAUE 1990).

Probably only the vibrational component of the sound acts as a defence against possible predators or parasitoids because the power maxima are at relatively low frequencies (1.00 kHz and 2.42 kHz). In this frequency range sound is best propagated through substrate vibration (see MARKL 1968, MASTERS *et al.* 1983). The emitted sound energy was not measured but must be very low since the sounds are nearly inaudible to the human ear.

The bioacoustic analysis refers only to female spiders. Male signals have not been analysed. Although there are no distinct morphological differences in the stridulatory apparatus of both sexes, differences in the resulting signal are still possible. Moving the plectrum more or less quickly across the file or across the two areas that show differences in rib size may lead to a distinctively different signal. We cannot deduce from the analysis of the defence sounds that the signal produced in intersexual (or intrasexual) contexts has similar characteristics. If *P. gibbulus* produces similar sounds during courtship and copulation then the mating partners could also use the vibrational components as signals and perceive them by means of the lyriform organs. However, the two mating individuals were observed to stridulate only when they were at a distance of less than 2 cm (if not in physical contact). This distance lies within the near field (radius < 1/6 of the wavelength). The animals can thus probably perceive

the sound velocity of the airborne component by means of their trichobothria. This mode of sound perception is often suggested for spiders but no reliable evidence has been reported (MARKL 1969; BARTH 1982).

Our findings concerning courtship display and mating position of *P. gibbulus* differ from GERHARDT's description (1927) in various aspects: he does not mention the courtship behaviour of the female and states that it is the male who ends copulation whereas we found that the female engages in courtship and may end copulation. Additionally, GERHARDT does not refer to any movements of the pedipalps that might be related to stridulation. Also, his description and drawing of the mating position differ somewhat from what we observed and he does not mention the locking mechanism of the male on the female during copulation in which the male's first pair of legs holds the female's fourth pair of legs.

In conclusion, the Palpimanidae are added to the list of 22 families of spiders in which stridulation is known to occur for at least some members of each family (UETZ & STRATTON 1982). The same applies to some other spider groups. Based on recent literature and some not previously cited, the following 8 families are added: Amaurobiidae (DAVIES 1986), Archaeidae (Millot 1948 in LEGENDRE 1970, FORSTER & PLATNICK 1984), Austrochilidae (FORSTER *et al.* 1987), Caponiidae (BRIGNOLI 1977, PLATNICK 1993, 1994*a,b*), Gradungulidae (FORSTER *et al.* 1987, DAVIES 1993), Mecysmaucheniidae (FORSTER & PLATNICK 1984), Pararchaeidae (FORSTER & PLATNICK 1984) and Stenochilidae (PLATNICK & SHADAB 1974), bringing the total to 31 families of stridulating spiders.

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